

Patterns of speciation in marine gastropods: A review of the phylogenetic evidence for localized radiations in the sea*

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Abstract: Modern speciation theory is heavily influenced by Mayr's postulate that prolonged geographical isolation is necessary for differentiated populations to evolve reproductive isolation. Present-day distributions of sister species are consistent with allopatric or peripatric speciation in many terrestrial and freshwater animal groups. However, the oceans present few obstacles to dispersal for marine taxa with planktonic larvae, and sister species are not often split at biogeographical breakpoints in the sea. Theory predicts that disruptive selection on habitat choice or resource use can split a population into divergent ecotypes without physical separation, yet sympatric speciation is still often viewed as improbable. Here, I review phylogenetic evidence from diverse marine gastropods to test Mayr's prediction that recently diverged sister species should not be sympatric over most of their ranges. In contrast to expectations, young sister species are often broadly sympatric in many gastropod groups, suggesting that classical models of allopatric divergence are insufficient to explain marine speciation. I discuss four mechanisms that may contribute to this deviation from predicted biogeographical patterns: transient allopatry along continuous coastlines, rapid evolution of gamete recognition proteins, shifts to non-planktonic development, and ecological divergence. The available evidence argues that patterns of marine speciation depend on complex interactions between geography, life history, and ecology, often resulting in local radiations within a basin or endemic to an island group. Whether selection acts on ecotypes in sympatry or on populations during secondary contact, ecological factors may promote speciation in the sea at smaller spatial scales than expected. I highlight areas for future study to improve our understanding of the forces generating marine biodiversity, and why the geography of speciation may be fundamentally different for shallow-water animals.

Key words: allopatry, biogeography, Mayr, ecological, sympatric speciation

"The range of the nearest relative of a given species is usually allopatric... This fact suggests that geographic speciation is the principal, if not exclusive, speciation mechanism in most marine animals." (Mayr 1954: 16)

An outstanding issue in evolutionary biology is whether the speciation process is fundamentally similar among marine, freshwater, and terrestrial animals (Valentine and Jablonksi 1983, Knowlton 1993, May 1994, Palumbi 1994, Briggs 2006). Mayr (1942, 1963) argued influentially that geographic structuring of terrestrial populations promotes divergence in allopatry and the development of intrinsic reproductive isolation over time. Ranges of terrestrial animals may be fractured by barriers to migration such as rivers and mountains, and island populations are inherently isolated from continental ancestors. Similarly, gene flow among lakes and drainage basins can be low for limnetic organisms with little ability to disperse over land. The fragmented nature of terrestrial and freshwater habitats is consistent with Mayr's observations that in groups such as birds, snails, and butterflies, contemporary

ranges of sister taxa are non-overlapping, and supported his postulate that speciation usually proceeds in allopatry. This view has become paradigmatic for marine taxa as well, despite the fact that the ocean has few obvious barriers to genetic exchange, and sister species are not always split by the thermal boundaries that demarcate regional faunas (Mayr 1954, Valentine 1966, Briggs 1974, Palumbi and Lessios 2005).

Mayr initially emphasized the primacy of geographic isolation in the early stages of speciation. However, mid-century studies on cichlids and phytophagous insects suggested that sympatric speciation was a viable model for divergence if novel ecotypes could emerge within a population (Thorpe 1945, Trewavas 1947). Mayr countered that ecology contributes to diversification while populations are spatially segregated and experiencing disruptive selection due to environmental differences between their habitats, such that isolation and differential adaptation go hand-in-hand: "all geographical races are also ecological races, and all ecological races are also geographical races" (Mayr 1947: 280). He held that populations overlapping in space would be segregated

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into different niches because ecological divergence was necessary for relatives to co-exist without competing, but argued that divergence precedes secondary contact.

In contrast, modern studies of speciation have focused on mechanism over geographical context, asking whether reproductive isolation arises as a product of natural selection, sexual selection, or the order and rate at which mutations occur and are fixed (by selection or drift) in isolated gene pools (Howard and Berlocher 1998, Turelli *et al.* 2001, Coyne and Orr 2004, Butlin *et al.* 2008, Schluter 2009). Ecologically based selection can promote pre-mating isolation in several ways, such as partitioning individuals by habitat or time of activity (Feder *et al.* 1994), removing maladapted immigrants before they can interbreed (Nosil *et al.* 2005), or reinforcement favoring assortative mating during secondary contact (Coyne and Orr 1989, 2004, Rundle *et al.* 2000, Servedio and Noor 2003, Rundle and Nosil 2005). Ecologically dependent post-mating isolation can arise when hybrids are unfit in parental environments (Egan and Funk 2009). Molecular evidence for positive selection on reproductive proteins, and on “speciation genes” involved in hybrid sterility or inviability, suggests protein evolution may commonly drive speciation (Swanson and Vacquier 2002, Tang and Presgraves 2009).

Reconstructing the dominant mode(s) of speciation in a given clade requires understanding the spatial arrangement of populations, and the timing of genetic changes that result in reproductive isolation. Determining the phylogeny and biogeography of extant taxa is needed to describe the spatial arrangement of related species, while ecological and breeding studies of putative incipient or recently diverged species can identify mechanisms that act during the early stages of speciation. Here, I review evidence from recent ecological and phylogenetic studies of marine gastropods to evaluate whether the data support Mayr’s proposal that speciation in the sea requires prolonged allopatry, and results in non-overlapping ranges of sister species. In the past two decades, molecular phylogenetic studies have provided robust hypotheses of evolutionary relationships that permit tests of Mayr’s prediction that genetic distance and range overlap should be positively correlated (Knowlton 1993, 2000). I will examine whether in gastropods, sister species or subspecies are usually allopatric, or frequently co-occur over most of their range. I first discuss four general mechanisms, not mutually exclusive, that may allow species to form in proximity and persist with largely overlapping ranges in the sea.

MECHANISMS THAT MAY RESULT IN SISTER SPECIES WITH SYMPATRIC DISTRIBUTIONS

Transient allopatry

Sea level fluctuations driven by Quaternary climate change may have caused transient allopatry for populations of benthic

invertebrates along continental margins, especially in intertidal and shallow subtidal habitats (Valentine and Jablonksi 1983, Reid 1990, Briggs 2006). During periods of low sea level, peripheral isolates may have been trapped in refugia where conditions were tolerable, perhaps enhanced by local adaptation to edge conditions or subtidal escape from stress. Long-separated populations may then have come into secondary contact during interglacials. In concert with ecological and reproductive mechanisms that inhibit gene flow, transient allopatry could produce distinctive phylogeographic patterns for coastal taxa in which closely related species have largely overlapping ranges, but discordant patterns of genetic polymorphism across their range (Marko 1998).

Non-planktonic development

For many marine animals, larval development determines the spatial scale at which gene flow occurs, profoundly affecting phylogeography and macroevolution (Strathmann 1978, McMillan *et al.* 1992, Hellberg 1996, Collin 2001, Jeffery and Emlet 2003). Loss of a planktonic larval stage may thus allow local adaptation and lead to speciation in geographical proximity. Planktotrophic larvae are transported by ocean currents for weeks to months while feeding, and are correlated with greater species longevity, larger ranges, genetically panmictic populations, and reduced adaptation to local conditions (Vermeij 1982, Caley *et al.* 1996, Bohonak 1999, Pechenik 1999). Lecithotrophic larvae can develop without feeding, and disperse for days to weeks (broadcast-spawning taxa), or minutes to days if larvae are released from egg masses or adult brood chambers. In non-planktonic development, juveniles emerge into the parental environment, decreasing the range and geological longevity of a species while promoting local adaptation (Hansen 1978, 1980, Jablonski 1986, Palumbi 1994, Todd *et al.* 1998, Sanford *et al.* 2003, Sanford and Worth 2009). Non-planktonic clades may also experience stronger effects of drift due to reduced effective population size, which could intensify divergence during transient allopatry through fixation of alleles that produce intrinsic isolation (Foltz 2003, Foltz *et al.* 2004). Shifts in development may thus have sweeping ecological and evolutionary consequences for marine taxa, a situation without parallel in terrestrial organisms.

Gastropod species with non-planktonic development accumulate over time in the fossil record, suggesting that lecithotrophic lineages may undergo species selection due to larval type, resulting in accelerated cladogenesis (Hansen 1978, 1980, Jablonski 1986). However, if non-planktonic development has frequent independent origins in a given group, non-dispersive lineages may accumulate over time without an increase in speciation rate (Duda and Palumbi 1999, Collin 2001). Phylogenetic studies offer the chance to test whether taxa with non-planktonic development undergo localized radiations resulting in young, sympatric sister taxa,

contrary to prevailing views of allopatric speciation. If so, loss of larvae may be a “speciation factor” (*sensu* Venditti *et al.* 2010) for some clades, but this has yet to be rigorously tested.

Fast-evolving gamete recognition proteins

The rapid divergence of gamete recognition proteins mediating sperm-egg fusion may allow incipient species of broadcast-spawners to co-exist without hybridizing, if mismatches among species produce pre-zygotic isolation (Palumbi 1994, 1999, Swanson and Vacquier 2002). Positive Darwinian selection, a “change is good” scenario at the amino acid level, has favored replacement substitutions in the bindin protein of echinoids and bivalves (Zigler *et al.* 2003, Moy *et al.* 2008). In vetigastropods, signatures of positive selection have been detected for sperm proteins (Swanson and Vacquier 1995, 1998, Hellberg and Vacquier 2000) and egg receptors (Galindo *et al.* 2003, Aagaard *et al.* 2006). Comparable studies have yet to be done on marine animals with internal fertilization, but gamete proteins rapidly diverge in terrestrial insects and mammals (Wyckoff *et al.* 2000, Swanson *et al.* 2001a, 2001b, 2003). Species-specific fertilization may rapidly arise by selection on proteins regulating sperm-egg recognition, permitting close relatives to persist in sympatry even if similar in niche and spawning behavior.

Ecological divergence

Mayr (1947) argued that both reproductive isolation and ecological divergence evolved while populations were geographically separated and were required for subsequent range overlap to develop. However, selection against ecologically intermediate hybrids can result when differentially adapted isolates come into secondary contact, driving the evolution of pre-mating barriers or post-zygotic isolation (Servedio and Noor 2003, McKinnon *et al.* 2004, Rundle and Nosil 2005, Funk *et al.* 2006, Egan and Funk 2009). Further, theory indicates disruptive selection on host, microhabitat or resource use can split one gene pool into two differentially adapted populations of non-competing specialists, even in the face of gene flow (Orr and Smith 1998, Dieckmann and Doebeli 1999, Kondrashov and Kondrashov 1999, Coyne and Orr 2004, Bolnick and Fitzpatrick 2007, Schluter 2009). Geographical isolation is not a requirement for speciation in such models, and sympatric divergence is greatly intensified if sexual selection acts on a condition-sensitive display trait (van Doorn *et al.* 2009).

Ecological speciation may be particularly likely if the trait under disruptive selection drives host or habitat choice and if individuals mate in preferred surroundings. Otherwise, recombination normally separates a trait and mating preference for that trait, inhibiting divergence (Rice 1984, 1987, Rice and Hostert 1993, Via 2001). If habitat choice produces assortative mating by pleiotropy, there is no selection-recombination antagonism, and disruptive selection

can further diversify incipient specialists through fixation of habitat-specific alleles (Diehl and Bush 1989, Bush 1994, Kawecki 1997, 1998).

Mayr foresaw such arguments nascent in the insect literature, and argued that recurring colonization of a novel host by the parental population, and back-colonization of the ancestral host, would effect gene flow to an incipient host race and thus hamstring divergence: “ecological isolation, in order to be effective, must be able to prevent the mixing of the to-be-separated populations in spite of dispersal” (Mayr 1947: 276). However, repeated invasion of a novel niche is unlikely if selection favors rapid shifts in reproductive and ecological characters following first colonization, as adapted specialists on the novel host would out-compete migrants from the ancestral host. The fly *Rhagoletis pomonella* formed distinct races on introduced apples, blueberries, and snowberries, with host fidelity and host-dependent selection limiting gene flow with populations on the native host; their parasites may also have speciated in sympatry (Feder *et al.* 1988, Filchak *et al.* 2000, Forbes *et al.* 2009). Pea aphids form distinct races on red clover and alfalfa, and gene flow is limited by habitat choice behavior of dispersing adults (Via 1999, Caillaud and Via 2000). Limnetic morphs of stickleback fish likely formed during secondary invasion of glacial lakes, after initial colonizers evolved into a benthic ecotype (Taylor and McPhail 2000). Barriers to gene flow can thus arise rapidly in response to diverse forms of selection and may produce different biogeographical patterns from those predicted from models of allopatric divergence.

Host shifting may be an important driver of speciation in insects, but divergent host use or microhabitat fidelity remains poorly studied for marine taxa (Frey and Bush 1990, Farrell 1998, Sotka 2005, Poore *et al.* 2008). Host shifts could occur among specialized epibionts such as barnacles that settle selectively on sponges, corals, snakes, or whales (Zann 2002). Commensal relationships may also impose selection for host specialization on marine taxa with a vagile adult stage, such as sponge-dwelling shrimp (Duffy 1996a, 1996b) and ophiuroids (Henkel and Pawlik 2005). Speciation by host shifting may be important for small-bodied and specialized consumers such as opisthobranchs (Faucci *et al.* 2007) and amphipods (Stanhope *et al.* 1993, Poore and Steinberg 1999, Sotka *et al.* 1999, Müller *et al.* 2000, Poore *et al.* 2000, 2008, Sotka 2005, 2007). Habitat partitioning along gradients in subtidal depth or intertidal stress represents another mechanism that could allow two populations to diverge within cruising range, if ecotypes are strongly segregated at small spatial scales (Mercurio *et al.* 1985, Davidson and Haygood 1999, Carlon and Budd 2002, Stillman 2002, Muths *et al.* 2006). However, such ecological associations have yet to be studied within an explicitly phylogenetic framework for marine taxa, to uncover potential drivers of speciation without prolonged isolation.

Substrate selection by larvae could be critical to ecological speciation in the sea, allowing genotypes to segregate at small spatial scales in a superficially well-mixed ocean. Due to their limited size and swimming speed, marine larvae have little control over large-scale movements, yet are remarkably adept at colonizing suitable habitat at small scales in response to habitat-specific chemical cues (Pawlik 1992, Krug 2001, Applebaum *et al.* 2002, Bierne *et al.* 2002, Baird *et al.* 2003). If adults maintain host or site fidelity, disruptive selection on larval habitat choice behavior could be a potent factor underlying ecological speciation. Adult microhabitat choice or homing behavior could also keep gene pools separate in the face of potential gene flow—for instance, allowing lineages of the tidepool copepod *Tigriopus californicus* to remain isolated on particular rocky outcrops for decades (Burton 1997).

INFERRING PATTERNS OF SPECIATION FROM RANGES AND PHYLOGENIES OF EXTANT GASTROPODS

Sister taxa that co-occur and occupy different niches did not necessarily speciate in sympatry. Ecological differences between sister species may have evolved (1) during transient allopatry in distinct environments, (2) by character displacement during secondary contact, or (3) from disruptive selection driving ecotype formation in sympatry. Distinguishing among these scenarios is difficult because ranges shift over time, so present-day overlap may not reflect the distribution of populations when speciation occurred (Barracough and Nee 2001, Losos and Glor 2003). However, simulations of divergence followed by range shifts indicate that contemporary range overlaps for sister species will have different statistical distributions for sympatric, allopatric, or peripatric speciation (Barracough and Vogler 2000). Phylogenies of birds, freshwater fish, and insects were consistent with expectations for allopatric speciation or peripatric divergence of range-edge populations, with only one case of fully sympatric, recently diverged sister species in *Rhagoletis* flies (Barracough and Vogler 2000). The available evidence for terrestrial and freshwater taxa is therefore consistent with Mayr's predictions. Below, I review phylogenies of marine gastropods to see if the distributions of recently diverged species deviate from expectations under a strictly allopatric model, a first step in identifying mechanisms that may promote speciation at different spatial or temporal scales in the sea.

Patellogastropoda

Molecular phylogenies of limpets reveal local radiations within the northeastern Atlantic (*Patella* Linnaeus, 1758, 9 spp.), northwestern Pacific (*Nipponacmea* Sasaki and Okutani,

1993, 8 spp.), and along the southeastern Pacific coast of Chile (*Scurria* Gray, 1847, 12 spp.). Two endemic radiations occurred in New Zealand, producing one clade of 8 *Cellana* Adams, 1869 spp. and a second clade of 13 *Notoacmea* Iredale, 1915 spp., a genus restricted to New Zealand except for 3 Australian species (Goldstien *et al.* 2006, Nakano *et al.* 2009). One recently derived pair of sister species was sympatric even at the microhabitat level in New Zealand. Smaller radiations of limpets were geographically restricted to southern Africa (*Scutellastra* Adams and Adams, 1854, 3 spp. and 5 spp.; *Cymbulla* Adams and Adams 1854, 3 spp.; *Helcion* Montfort, 1810, 3 spp.), and the southeastern Pacific (*Nacella* Schumacher, 1817, 3 spp.) (Nakano and Ozawa 2004, 2007). In *Lottia* Gray, 1833 six pairs of sister species are broadly sympatric in the northwestern Pacific, northeastern Pacific, or Western Australia; however, many other sister species remain allopatric (Nakano and Ozawa 2007).

Patterns of speciation may be different for temperate versus tropical lineages (Paulay and Meyer 2002). For instance, among 18 species of *Patelloida* Quoy and Gaimard, 1834 found in the tropical Indo-Pacific, most lineages are allopatric and restricted to distinct archipelagos (Kirkendale and Meyer 2004). Coastal taxa may therefore exhibit distinct biogeographic patterns compared to the fauna of tropical islands. However, phylogenetic evidence indicates at least some limpets speciate in a manner contrary to the expectations of strict allopatry since close relatives co-occur in most genera and whole clades may be limited to the same region or coastline.

Ecological speciation has long been suggested as a mechanism underlying sympatric diversification in limpets, which vary in their degree of substrate specificity (Test 1945, Kimberly *et al.* 1985). Limpets exhibit microhabitat-associated ecotypes or morphological plasticity, such as the barnacle and rock forms of the overlapping sister species *Lottia digitalis* Rathke, 1833 and *L. austrodigitalis* Murphy, 1978 (Crummett and Eernisse 2007). Other species display specificity for a particular substratum or host, including wood (*Pectinodonta* Dall, 1882; Lindberg 1990), shells of bivalves (*L. pelta* Rathke, 1833; Mercurio 1985) or gastropods (*L. asmi* Middendorff, 1847; Lindberg 1990), brown algae (*L. incessa* Hinds, 1842 on *Egregia* Areschoug, 1876; Choat and Black 1979), and seagrasses (*L. alveus* Conrad, 1831 on *Zostera*, *L. paleacea* Gould, 1853 on *Phyllospadix*; Lindberg 1981, Carlton *et al.* 1991). Ecological study of incipient or recently diverged species could shed light on the potential role of selective factors in promoting reproductive isolation in patellogastropods. Alternatively, population genetic studies of temperate limpet species could also test predictions for speciation by transient allopatry, such as reduced genetic diversity in newly colonized overlap regions compared with peripheral refugia.

Vetigastropoda

Tegula Lesson, 1832

Hellberg (1998) analyzed relationships among 23 of 40 *Tegula* spp., a genus about 15 million years old. McLean (2007) recently moved the temperate species *T. brunnea* Philippi, 1848, *T. montereyi* Kiener, 1850, and *T. funebris* Adams, 1855 to *Chlorostoma* Swainson, 1840 (previously a subgenus) due to differences in columellar morphology between tropical and temperate species. However, according to phylogenetic analyses in Hellberg (1998), this would render *Chlorostoma* either polyphyletic or paraphyletic with respect to *Tegula*. Pending a major revision of this group, I retain the use of *Tegula* for discussion of Hellberg (1998); however, his conclusions about the geography of speciation were based on relationships of temperate species and should be unaffected by the above-mentioned taxonomic changes.

Phylogenetic evidence argued against vicariant severance of connections across the north Pacific, instead revealing separate radiations on each side of the basin. Three clades in the north Pacific were restricted to single coastlines in California, Baja California, and eastern Asia. Five of six sister species pairs were broadly sympatric. Sister taxa were not separated by apparent biogeographical barriers such as the East Pacific deep water, north Atlantic cold water, Isthmus of Panama, or Point Conception, California. The monophyly of sympatric clades was not an artifact of incomplete taxon sampling, as all north Pacific *Tegula* spp. were included. The lone example of allopatric sister species concerned a pair found along the outer coast of Baja and in the upper Sea of Cortez. However, this pair may have had overlapping ranges until closure of the cross-Baja seaway 1 mya; further, they are the most genetically distant pair, which is the opposite of Mayr's prediction that closest relatives should be allopatric.

What fueled diversification along coastlines in *Tegula*? Larval development cannot be invoked, as *Tegula* spp. are broadcast spawners with a moderate larval period of 5–13 days. For taxa along continental margins, sea-level fluctuations may commonly yield overlapping distributions if secondary contact is an inevitable consequence of range expansion after transient allopatry—a “nowhere to hide” scenario (Valentine and Jablonski 1983, Reid 1990, Hellberg 1998). However, Pleistocene range shifts did not sunder one pair of sympatric *Tegula* spp. along the eastern Pacific (*T. brunnea* and *T. montereyi*). The sperm protein lysin undergoes rapid evolution by positive selection in *Tegula*, which may allow young species to coexist if fertilization blocks arise quickly in peripheral or transient isolates (Hellberg and Vacquier 2000). Alternatively, ecological speciation in sympatry may have occurred through microhabitat specialization and differential adaptation to gradients in the physical environment of the rocky intertidal

(Riedman *et al.* 1981, Tomanek and Somero 1999, 2000, Tomanek 2002).

Astraliium rhodostomum Lamark, 1822 (Turbinidae)

A different pattern of lineage distribution was described for the widely distributed tropical snail *Astraliium rhodostomum* (Meyer *et al.* 2005). A phylogeographic study of this nominal species uncovered two clades broadly sympatric across the Indo-Pacific, each containing 30 discrete mitochondrial lineages restricted to a particular island. No appreciable gene flow occurred over as little as 180 km, likely due to a larval period lasting only a few days. The persistence of young lineages with restricted and allopatric distributions is consistent with Mayr's paradigm although the two cryptic species (Clade A and B) described by Meyer *et al.* (2005) were widely sympatric across the tropical Indo-Pacific. Without knowing when reproductive isolation evolves in the lineage sorting process, it remains difficult to assess whether biologically “good” species of turbinids evolve in strict allopatry or parapatry, obscuring the geography of speciation. However, taxa native to tropical archipelagoes exhibit genetic patterns that are different from those living on north-south coastlines (Paulay and Meyer 2002).

Haliotis Linnaeus, 1758

Abalone are broadcast-spawning vetigastropods in which closely related species often co-occur. Seven *Haliotis* spp. are found in California, partly or broadly overlapping in ecological niche, depth zonation, and breeding season. Hybridization can be forced in the lab at high sperm concentration but rarely occurs in the field. Phylogenetic analyses indicate one radiation of 4 species and an independent origin of a further two sister species in California, with additional radiations in Japan (3 species) and Australia (6 species) (Lee and Vacquier 1995, Yang *et al.* 2000). This taxon therefore shows a pattern opposite to that expected under allopatric divergence: close relatives occur in sympatry, and more distant relatives are predominantly allopatric.

Abalone thus represent a conundrum: how do sympatric lineages maintain species integrity when gametes are shed into the ocean at the same time of year? Sperm chemotaxis is species-specific in abalone, but explains only a fraction of the pre-zygotic isolation between two species (Riffell *et al.* 2004). The biochemistry of fertilization has been well studied in abalone, offering a mechanistic understanding of gamete interactions (Swanson and Vacquier 2002). The soluble protein lysin is released from the sperm acrosome and binds to an egg receptor (VERL), causing dissolution of the egg envelope; lysin binding is highly species-specific, and lysin protein sequences diverge rapidly among species (Swanson *et al.* 2001c). The sperm protein sp18 mediates gamete fusion, and its coding sequences are also under strong positive

selection (Swanson and Vacquier 1995). Both proteins are among the fastest evolving genes known, with substitution rates 20 times higher in coding than noncoding sequences (Metz *et al.* 1998). Much of VERL evolves neutrally by concerted evolution, but the amino-terminal end diverged rapidly among species by positive selection (Swanson and Vacquier 1998, Galindo *et al.* 2003). Signatures of adaptive molecular evolution were also detected in 6 of 10 proteins containing zona pellucida domains from the abalone egg jelly coat (Aagaard *et al.* 2006).

Comparison of 25 *Haliotis* spp. revealed that lysin is under strong selection for amino acid substitutions, but replacement rates vary among lineages (Yang *et al.* 2000). Non-synonymous changes accumulated most rapidly among sympatric lineages; rates of molecular evolution were lowest along branches separating distantly related or allopatric lineages. These findings are consistent with the postulate that reproductive isolation can evolve rapidly via selection on gamete recognition proteins among sympatric species. The analysis could not distinguish whether accelerated protein evolution was a consequence of sympatry or a precondition allowing related species to co-occur. However, radiations along a coastline appear to be common in the marine realm, even with little ecological diversification, provided there are other mechanisms by which selection can drive reproductive isolation.

Caenogastropoda

Calyptraeidae

Collin (2003) produced a well-resolved phylogenetic hypothesis for 84 ingroup taxa comprising distinct species or divergent populations of calyptraeid slipper shells, a group of sessile, filter-feeding caenogastropods. Of 29 identified sister-species pairs, 11 are sympatric, and all recently diverged sister species (pairwise Bayesian distance of <5%) are either fully sympatric or in close geographic proximity. A further 10 clades (3-9 species each) are found along a single coastline, including species with overlapping ranges. Overall, 72% of sister species are in close proximity to their nearest relative(s) in the absence of any major barrier, with none separated by the Isthmus of Panama, the eastern Pacific deep water, or the Benguela upwelling.

Despite the prevalence of local speciation in the calyptraeids, only one large radiation was restricted to a single region, a clade of eight species with non-planktonic development in the northeastern Pacific (Collin 2004). Non-dispersive development likely fueled speciation in this localized radiation. Outside of this clade, however, only one pair of sister species shared non-planktonic development; thus, reduced dispersal is not generally responsible for co-occurrence of sister taxa in the Calyptraeidae. It is unclear

what factors contribute to the high frequency of sympatric sister species throughout the slipper shells. All calyptraeids are sessile filter-feeders, so shifts in trophic ecology are not a viable explanation. Collin proposed transient allopatry or microhabitat partitioning as possible explanations, but further study is needed.

Cypraeidae

From a phylogenetic perspective, cowries are one of the most rigorously studied and well-sampled groups. Meyer (2003) identified evolutionarily significant units (ESUs) as unique mitochondrial lineages that correspond to species, subspecies, or regional populations with a long history of isolation. The majority of cypraeid biodiversity lies in the tropical Indo-West Pacific (IWP), where 12 low-diversity lineages contain 1-3 widely distributed species lacking phylogeographic structure; a few have peripheral endemics. Six lineages contribute 5-26 allopatric ESUs apiece, most showing reciprocal monophyly between basins, concordant with Mayr's proposal that recently evolved sister groups be non-overlapping.

A single lineage, the Erroneinae (130 spp.), represents over half the IWP species diversity in the Cypraeidae. Most species have small ranges and show reciprocal monophyly between basins; only *Talostolida pellucens* Melvill, 1888 has an extensive range with no genetic structure. Based on protochonch morphology, Meyer proposed this group has reduced planktonic dispersal potential but retains a swimming larval stage. Limited potential for dispersal and allopatric diversification among archipelagos likely accounts for the species diversity in this group, as in the turbinid *Astraliium rhodostomum*; over half the divergence events in the IWP were allopatric, based on the retained signal of geographical speciation in extant taxa. Peripatric speciation is implicated by the presence of numerous paraphyletic peripheral isolates at the edge of a parent species' range, consistent with theory that this is a common mode of speciation in diverse taxa (Barracough and Vogler 2000).

Despite the clear evidence for allopatric speciation in the tropics, cowries also illustrate how loss of a dispersive larval stage may spur local cladogenesis. Non-planktonic development evolved at least five times in the Cypraeidae, always on upwelling coastlines such as southern Australia (*Zoila* Jousseaume, 1884, *Umbilia* Jousseaume, 1884, *Austrocypraea* Cossmann, 1903, and *Notocypraea* Schilder, 1927), southern Africa (*Barycypraea* Schilder, 1927, *Cypraeovula* Gray, 1824), and the northern coast of Columbia and Venezuela (*Muracypraea* Woodring, 1957) (Meyer 2003). Radiations along a single coast occurred in three Australian genera (*Zoila*, 11 spp.; *Umbilia*, 3 spp.; *Notocypraea*, 5 spp.) and the South African genus *Cypraeovula* (14 spp.). Loss of larval dispersal

may simply reduce the spatial scale at which allopatric divergence occurs, or could magnify the effects of local selection and facilitate ecological speciation (see *Littorina*, below). Further study of ecological differences among species in these local endemic flocks is therefore warranted.

Conus Linnaeus, 1758

The hyper-diverse genus *Conus* contains >500 species of predatory cone snails, mostly tropical with 60% of species found in the IWP (Kohn and Perron 1994, Röckel *et al.* 1995). Most species are specialized to feed on either fish, molluscs, worms, or hemichordates, injecting paralytic peptides (conotoxins) through a hollow radula (Kohn and Perron 1994). The degree of specialization on subtypes of the four general prey categories varies among cone snails, but if disruptive selection acted on resource use, cone snails could be candidates for ecological speciation. However, a phylogenetic analysis of 76 *Conus* spp. revealed instead that the same prey type is shared by all unambiguous sister species and often across larger clades (Duda *et al.* 2001). The ancestral condition was likely worm-feeding with 2–4 independent origins of fish predation and one switch to mollusc predation (Duda and Palumbi 2004). Leviten and Kohn (1980) also reported no ecological differences in microhabitat resource use among co-occurring *Conus* spp.

Despite the lack of evidence for speciation by diet shift, a subsequent phylogenetic study of 138 *Conus* spp. revealed that many sister taxa are broadly sympatric in regions such as the Caribbean (*C. lorenzianus* Dillwyn, 1879 + *C. spurius* Gmelin, 1791; *C. mindanus* Hwass in Bruguière, 1792 + *C. jaspideus* Gmelin, 1791; *C. daucus* Hwass in Bruguière, 1792, *C. villepinii* Fischer and Bernardi, 1857 + *Conus* sp. WA-1), the eastern Pacific (*C. lineolatus* Valenciennes, 1832 + *C. princeps* Linnaeus, 1758; *C. bartschii* Hanna and Strong, 1949 + *C. bruneus* Wood, 1828), and eastern Africa (*C. ateralbus* Kiener, 1845 + *C. cuneolus* Reeve, 1843) (Duda and Kohn 2005). The IWP also holds numerous sympatric sister species or radiations, including two sister pairs of worm-feeders (*C. chaldaeus* Röding, 1798 + *C. ebraeus* Linnaeus, 1758; *C. coffeae* Gmelin, 1791 + *C. tenuistriatus* Sowerby, 1858), a clade of six worm-feeders, and a clade of seven fish-eaters. Some closely related sister taxa (*C. frigidus* Reeve, 1848 + *C. sanguinolentus* Quoy and Gaimard, 1834 + *C. eburneus* Hwass in Bruguière, 1792 + *C. tessulatus* Born, 1778) specialize on different types of worms, offering the possibility that disruptive selection on resource use fueled divergence although ecological character displacement after secondary contact is also viable.

Perhaps the most dramatic example of a marine “species flock” (a highly localized radiation) is the diversification of *Conus* in the Cape Verde islands off the western coast of Africa. Of 50 *Conus* spp. in the archipelago, 47 are endemic

and fall within one or two clades, pending resolution of phylogenetic ambiguity (Duda and Rolan 2005). The radiation in Cape Verde was so recent that some species cannot be distinguished at the fast-evolving mitochondrial cytochrome *c* oxidase I locus, but are ecologically or morphologically distinct. Most species are restricted to one or two islands, and all but *C. damottai galeao* Rolán, 1990 are sympatric with their sister taxon. Rapid cladogenesis on Sal Island resulted in a clade of nine recently diverged species. All 47 Cape Verde endemics have non-planktonic development, further evidence that loss of a planktonic larval stage is correlated with local endemic radiations.

Overall, phylogenetic analyses reject both extreme models of cone snail evolution—that sister species will either be allopatric, or sympatric but differing in resource use. In fact, most cone snails overlap in range but also in prey type with their sister taxon. Future studies of ecology and phylogeography are needed to explore the mechanism(s) behind cone snail diversity. Adaptive evolution of amino acid sequences of the conotoxins offer potential insight into ecological specialization at the molecular level in this group (Remigio and Duda 2008).

Echinolittorina Habe, 1956

The circumtropical genus *Echinolittorina* is restricted to rocky shores, with maximum diversity in the tropical IWP (Williams and Reid 2004). Larvae develop during a four-week planktonic period. Of 59 ESUs identified by genetic analysis, sister species are mainly allopatric, including 7 of 8 pairs in the IWP and 8 of 12 in the eastern Pacific/Atlantic (Williams and Reid 2004). At deeper nodes, about two-thirds of sister clades are geographically partitioned among ocean basins. As predicted by Mayr, the percentage of range overlap is positively correlated with genetic distance in the IWP, where there were no overlapping sister species in archipelagos. Most peripheral IWP species are range-restricted endemics. Most if not all sister taxa are also allopatric in the Caribbean. In contrast, four pairs of recently diverged sister species are broadly sympatric along an eastern Pacific coastline, and one such pair occurs in Asia (Williams and Reid 2004).

The long-term persistence of allopatry in this group may reflect a planktonic larval duration long enough to impede local adaptation, which may otherwise accelerate divergence in transient allopatry or sympatry. Williams and Reid (2004) also proposed that differences between continental shelf versus oceanic island habitats may act as a barrier to dispersal, along with stretches of inhospitable coastline lacking suitable rocky habitat. Different patterns in the IWP and Caribbean versus the coastal Eastern Pacific support the contention that speciation patterns differ between archipelagos and continental margins (Paulay and Meyer 2002).

Nucella Röding, 1798

Dog whelks in the genus *Nucella* comprise six northern Pacific and one northern Atlantic species (Collins *et al.* 1996). All species have non-planktonic development with crawl-away juveniles and are restricted to rocky intertidal habitats. Three members of one clade (*N. lamellosa* Gmelin, 1791, *N. canaliculata* Duclos, 1832, and *N. ostrina* Gould, 1852) are sympatric over most of their ranges from Alaska to northern or central California (Collins *et al.* 1996, Marko and Vermeij 1999, Marko *et al.* 2003). The southern *N. emarginata* Deshayes, 1839, ranging from central California to Baja California, Mexico, shares a recent ancestor with *N. ostrina*, and their mitochondrial haplotypes have not completed lineage sorting. These sister species overlap throughout central California but are habitat partitioned, with *N. ostrina* found in more wave-exposed sites and *N. emarginata* in shallower, less disturbed sites (Marko 1998). Central California populations of *N. emarginata* have reduced genetic diversity at allozyme and mitochondrial loci, suggesting a northward range expansion from a high-diversity Baja population in the late Pleistocene. Similarly, populations of *N. ostrina* from central California have higher diversity and more genetic structure than in the northern half of the range, suggesting a recent expansion of *N. ostrina* along Canadian and Alaskan shores (Marko 2004). In contrast, *N. lamellosa* retains significant genetic structure and diversity across its range, indicating a history of persistence in northern glacial refugia (Marko 2004).

Together, genetic data suggest the deeper-dwelling *Nucella lamellosa* survived in Alaska and Canada during periods of low sea level and cold temperatures, when *N. ostrina* was likely restricted to central California and *N. emarginata* to the Baja Peninsula. Range contractions due to climate change may thus have trapped isolates long enough for reproductive isolation to arise, followed by range expansions that led to secondary contact and present-day sympatry. Population genetic data can therefore provide valuable insight into historical demographics and range dynamics, and can be used to test hypotheses about mechanisms of speciation along north-south coastlines.

Littorina Férussac, 1822

A group of ecologically well-studied gastropods, *Littorina* (19 spp.) are found on rocky shores in the northern Pacific and northern Atlantic (Reid 1996). Phylogenetic hypotheses based on morphology and gene sequences for three loci were largely congruent (Reid *et al.* 1996). In the northern Pacific, 2-3 sister species pairs (*L. brevicula* Philippi, 1844 + *L. mandshurica* Schrenk, 1861; *L. sitkana* Philippi, 1846 + *L. horikawai* Matsubayashi and Habe in Habe, 1979; and likely *L. aleutica* + *L. natica*) have overlapping range edges but are not broadly sympatric. In contrast, sisters *L. squalida* Broderip

and Sowerby, 1829 and *L. littorea* Linnaeus, 1758 are fully allopatric (Reid *et al.* 1996). In the eastern Pacific, sister species *L. scutulata* Gould, 1849 and *L. plena* Gould, 1849 are broadly sympatric along California. Phylogenies of Pacific *Littorina* are consistent with vicariance induced by climate change causing peripheral isolation in range-edge refugia, and speciation in transient allopatry (Reid 1990).

In the Atlantic, there are two clades each composed of sympatric species. *Littorina obtusata* Linnaeus, 1758 and *L. fabalis* Turton, 1825 co-occur on both northern Atlantic coasts, while *L. compressa* Jeffreys, 1865, *L. arcana* Ellis, 1978, and *L. saxatilis* Olivi, 1792 are sympatric in the northeastern Atlantic. It is not clear how vicariance could produce the observed species distributions in the northern Atlantic; however, ecological speciation provides an alternative explanation (see below). Further, these five northern Atlantic species all have non-planktonic development, an additional factor that could contribute to the concentration of related species in this region (Reid *et al.* 1996).

Littorina saxatilis has emerged as a model organism for ecological speciation studies (Johannesson 2001). Development is non-planktonic, and adult migratory ability is limited to a few meters per month (Johannesson *et al.* 1993). Within populations, there are steep microclines in morphology and genetics along vertical tidal gradients. Differential selection favors large, banded, and ridged shells for the ecotype living among barnacles in the upper tidal zone; a smaller, smooth morph predominates in the low-water mussel zone (Johannesson *et al.* 1993). In Sweden, hybrid snails with intermediate characters occur in barnacle-to-mussel transition zones, where they may have a fitness advantage over pure parental types (Janson 1983). In Spain, hybrids are rare and selection favors different alleles of the aspartase aminotransferase enzyme across a three-meter transition zone (Johannesson *et al.* 1995a).

In Spain, three factors underlie reproductive isolation between the morphs (Johannesson *et al.* 1995b). First, pure ecotypes aggregate through microhabitat choice, clustering together even in the mid-shore transition zone where available habitat is a mosaic of mussel and barnacle patches. Thus, the two morphs do not encounter each other frequently, even when intermingled mid-shore. Snails also aggregate by size within morphs at all shore levels. Second, pairs mate assortatively in the field, even after controlling for micro-distributional bias, indicating a behavioral component of mate choice. Pure-by-hybrid pairs conform to a random distribution in the transition zone, however, and mating between pure morphs is also random in the lower zone due to the rarity of the upper-shore ecotype; such cross-morph matings cause limited gene flow between the pure morphs. Third, hybrid females have lower fitness than the upper-shore morph.

It was initially unclear if size-assortative mating was a pleiotropic effect of selection on size due to microhabitat use, or a behavioral response to selection against hybrid offspring. Pure ecotypes survival is highest in their home zone, lowest in the opposite zone, and intermediate in the transition zone (Rolán-Alvarez *et al.* 1997). However, hybrid survival is equivalent at all tidal heights and equal to that of pure morphs in the transition zone. Since hybrids are as fit as pure morphs, assortative mating likely evolved as a pleiotropic effect of selection on other characters and not to selection against hybridization. Genetic studies further suggest that ecotypes evolved in parallel at multiple sites under the same selective pressure (Rolán-Alvarez *et al.* 2004).

Different conclusions were reached for British *Littorina saxatilis* present as distinct shell morphs on a cliff side versus rock cobble (Grahame *et al.* 2006). Where the two habitats abutted, a cline in shell morphology was congruent with a genetic discontinuity. A sharp break in allele frequencies was detected at 15 loci thought to be under strong selection, and analysis of 275 undifferentiated loci supported a general barrier to gene flow across the habitat cline. Grahame *et al.* (2006) argued this pattern reflects allopatric divergence, secondary contact, and introgression. They disputed parallel divergence of Spanish *L. saxatilis* on the grounds that rare long-distance dispersal and colonization events were alternative explanations for the co-existence of ecotypes (see also Butlin *et al.* 2008).

Spanish hybrid zones in *Littorina saxatilis* are of “primary origin” if they arose in parallel via sympatric divergence of ecotypes; alternatively, the two ecotypes may have evolved one or more times in allopatry, with present-day overlap zones reflecting secondary contact. Quesada *et al.* (2007) sequenced 1.83 kb of mitochondrial DNA to distinguish between these competing hypotheses. Genetic data revealed strong differentiation among four sites with locally restricted haplotype clades, yet many polymorphisms and even haplotypes were shared between ecotypes within a site. Coalescent estimates suggested ecotypes diverged in parallel at each site within the last 40,000 years, as *L. saxatilis* spread south along the Galician coast (Quesada *et al.* 2007). Genetic and experimental evidence in Spain thus support repeated, sympatric divergence of ecotypes due to strong selection across an environmental cline, with assortative mating evolving as a byproduct of selection on traits associated with habitat use.

Sadedin *et al.* (2009) modeled the evolution of ecotypes and assortative mating to explore the range of parameters that favored speciation in the *Littorina* system. In simulations, ecotypes often evolved under ecologically relevant values for the strength of selection, number of loci influencing ecologically key traits, mate choice system, size of the hybrid zone, and source of asymmetry in population density. Ecotype

formation was limited not by gene flow, but by selection impeding colonization of alternative tidal zones by one morph, genetic systems where traits were controlled by many loci of small effect, or frequent long-distance dispersal that reduced genetic structure (Sadedin *et al.* 2009). After ecotype formation, symmetric assortative mating evolved often but did not always increase in strength; assortative mating could evolve transiently or persist long term without leading to speciation, especially if selection favored a zone of hybrid superiority like in Swedish *L. saxatilis* (Sadedin *et al.* 2009). However, strength of assortative mating increased over time in some simulations. Thus, depending on the interplay of selection, quantitative genetics, dispersal and mate choice, ecotypes can be an evolutionarily stable state or an intermediate in the process of sympatric speciation via disruptive selection.

Heterobranchia

Chromodorididae

Until recently, the colorful chromodorid nudibranchs and their relatives were thought to comprise a few speciose genera, each with representatives in several ocean basins, and several less diverse genera with restricted distributions. Molecular phylogenetic analysis revealed instead that traditional genera are not monophyletic; eastern Atlantic species of *Hypselodoris* Stimpson, 1855 are not reciprocally monophyletic with respect to Indo-Pacific congeners, and species of *Mexichromis* Bertsch, 1977 in the western Atlantic and eastern Pacific are not sister groups (Wilson and Lee 2005, Turner and Wilson 2008). Despite long-standing assumptions about the influence of vicariance on biogeography, sister species of chromodorids are sympatric in many clades, and local radiations have occurred along single coastlines. For instance, *Chromodoris purpurea* Risso in Guérin, 1831 and *C. krohni* Verany, 1846 are sympatric in the eastern Atlantic and Mediterranean, as are four *Hypselodoris* species (*H. bilineata* Pruvot-Fol, 1953, *H. orsiui* Verany, 1846, *H. picta* Schultz, 1836, and *H. villafranca* Risso, 1818). All three known species of *Digidentis* co-occur in southeastern Australia (Turner and Wilson 2008). Numerous radiations also occurred within the tropical IWP.

Because chromodorid nudibranchs can be highly stenophagous, specializing on particular species of chemically defended prey sponges, ecological speciation by resource partitioning is one possible explanation for speciation in sympatry. Further ecological study of nudibranch resource utilization, depth zonation, and larval development may reveal whether sympatric ecological specialization or transient allopatry can explain the co-occurrence of sister taxa. For example, four species of *Chromodoris* (*C. tasuaniensis* Bergh, 1905, *C. epicurea* Basedow and Hedley, 1905, *C. daphne*

Angas, 1864, *C. splendida* Angas, 1864) are sympatric in eastern Australia, but as at least three feed on the same sponge species, ecological divergence is not a viable explanation. Questions worthy of investigation include how close relatives can (1) co-exist without hybridizing, and (2) occupy the same specialized niche without one out-competing the others.

Morphological study suggested that the direct-developing nudibranch *Doris "kerguelensis"* Bergh, 1884 was one widespread species with a circumpolar distribution around Antarctica (Wägele 1990). However, molecular data revealed an extraordinary radiation of 29 putative cryptic species (17 occurring in Bransfield Strait alone), with rarefaction analysis suggesting many more yet to be found (Wilson *et al.* 2009). Transient isolation of lineages in multiple refugia during Pleistocene glaciation cycles may have fueled this radiation in the Southern Ocean. Non-planktonic development is also implicated as a factor underlying rapid, local cladogenesis in this putative species flock.

Phestilla Bergh, 1874

Nudibranchs in group Aeolidina are specialized predators of cnidarians and show a range of coevolved adaptations to their prey, including sequestration of cnidae (Greenwood and Mariscal 1984, Martin 2003), retention of diet-derived zooxanthellae (Rudman 1981, Burghardt *et al.* 2005, 2008), and crypsis (www.seaslugforum.net/message/13424). Despite the potential for ecological speciation among aeolids, little attention has gone to the role of host shifting in their lineage diversification. Faucci *et al.* (2007) presented a phylogeny of the coral-eating nudibranch genus *Phestilla*. Although no ancestral character state reconstructions were performed, their data suggest that the ancestral *Phestilla* fed on a species of the hard coral *Porites*, as do all extant species except a derived pair of sister species that feed respectively on *Tubastrea* Lesson, 1829 (*P. melanobranchia* Bergh, 1874) and *Goniopora* de Blainville, 1830 (undescribed *Phestilla* sp. 2; Faucci *et al.* 2007). Additional studies are needed to test whether host shifting is a viable mechanism for speciation among aeolid nudibranchs.

Sacoglossa

The Sacoglossa are a clade of small-bodied, mainly herbivorous sea slugs that feed suctorially on large-celled, typically siphonaceous host algae; two genera feed on eggs of other opisthobranchs, and a few species radiated onto marine angiosperms or diatoms (Jensen 1983, 1996, Trowbridge 2002). Most sacoglossans are host restricted, feeding on one algal genus or a preferred species, making the Sacoglossa one of the only groups of specialized marine herbivores (Jensen 1989, Trowbridge 1991, Trowbridge and Todd 2001, Poore *et al.* 2008, Trowbridge *et al.* 2008, Baumgartner *et al.* 2009,

2009, 2010). The radula of a given sacoglossan species may be adapted to the host alga's cell wall, and slugs typically sequester defensive toxins from their host (Cimino and Ghiselin 2009). Members of the speciose clade Plakobranchoidea retain functional chloroplasts from their diet, and a few acquired functional algal genes through lateral gene transfer (Pierce *et al.* 2003, Händeler *et al.* 2009, Schwartz *et al.* 2010). Larvae of some sacoglossans metamorphose in response to host-specific chemical cues, further evidence of coevolution between slug and host (West *et al.* 1984, Krug and Manzi 1999, Krug 2001; but see Trowbridge and Todd 2001).

Sacoglossans thus show specialized associations analogous to those of phytophagous insects and angiosperms. Further, sympatric congeners are often partitioned onto different host algae, making sacoglossans a model system for investigating whether host shifts facilitate speciation. Phylogenetic and ecological studies currently underway suggest that host shifting has occurred pervasively over the evolutionary history of the shell-less sacoglossans, and has been a key driver of diversification in the speciose genus *Elysia* Risso, 1818 (Krug, Rodriguez, Trathen, Ellingson, and Trowbridge, unpubl. data). For example, out of 54 *Elysia* spp. studied to date, the most recently diverged sister species (*E. pratensis* Ortea and Espinosa, 1996 and *E. subornata* Verrill, 1901) co-occur throughout the Caribbean and are sympatric in the same habitat, but are partitioned onto different host algae. Despite a history of hybridization and mitochondrial introgression, they remain distinct in morphology and in their nuclear genome (Rodriguez 2009). Ecological speciation in sympatry is a viable explanation when recently divergent taxa have entirely overlapping ranges yet maintain species integrity despite hybridization due to differential resource use and habitat association. Cycles of niche expansion and contraction, potentially driven by changing tolerance for chemical defenses, may underlie host shifts in sacoglossans as has been proposed for terrestrial insects (Camara 1997, Janz *et al.* 2006).

In some cases, however, sympatric and congeneric sacoglossans may share the same host (Trowbridge *et al.* 2008, 2009, 2010). A robust phylogeny is needed to resolve whether co-occurring species are generally (a) host-partitioned sister taxa, as predicted by ecological speciation; (b) host-sharing but not closely related, as predicted by Mayr; or (c) host-sharing sister taxa, which are not predicted by either model. The last prediction, if borne out, would suggest that contrary to classical ecological theory, there is little competitive exclusion among these small-bodied herbivores. Ongoing studies will test whether host shifting and host diversity are drivers of speciation in sacoglossans, and will facilitate comparisons between specialized herbivores in marine and terrestrial systems (*e.g.*, Becerra 1997, Cook *et al.* 2002, Janz *et al.* 2006, Leschen and Buckley 2007).

CONCLUSIONS

Phylogenies of diverse marine gastropods show that recently diverged sister species are often sympatric, especially along temperate coastlines, in the Caribbean, and on remote island chains (Table 1). This contrasts sharply with the distribution of sister species among terrestrial faunas, and with predictions under models of allopatry with subsequent range shifts. Taxa with centers of diversity in the Indo-West Pacific, such as cone snails and cowries, exhibit species distributions that are consistent with models of allopatric divergence, but even in these groups endemic radiations occur in peripheral regions. Future tests comparing distributional patterns against statistical null models are therefore warranted for marine animals, especially where plausible alternative

models can be invoked, such as ecological speciation in sympatry.

In groups like *Nucella* and *Echinolittorina*, transient allopatry may explain the overlapping ranges of related species along north-south coastlines. Range shifts following peripheral isolation during Pleistocene glacial-interglacial cycles should leave genetic signatures that may allow tests of this model. In broadcast-spawners such as *Haliotis* and *Tegula*, the rapid divergence of gamete recognition proteins among transiently allopatric populations may allow recently diverged or incipient species to co-occur without fusing back into one gene pool. Selection favoring amino acid changes may thus act during secondary contact to confer reproductive isolation, and produce the observed patterns of sympatric overlap. Whether positive selection also drives functional diversification of sperm

Table 1. Summary of distributional patterns of sister species in marine gastropods for which detailed molecular phylogenies exist. Check-marks indicate whether the majority of studied species broadly overlap with their closest relative or remain allopatric. An "X" denotes evidence for a mechanism that could promote divergence or co-existence of young sister species in sympatry, while a "?" denotes a suggested mechanism for which evidence is lacking. Parenthetical notes refer to specific cases discussed in the text for that group.

Taxon	Sister taxa primarily allopatric	Sister taxa frequently sympatric	Potential mechanism behind sympatric distribution of sister taxa			
			Transient allopatry	Benthic development	Gamete recognition	Ecological divergence
Patellogastropoda	✓ (tropical)	✓ (temperate)	?			?
Vetigastropoda						
<i>Tegula</i>		✓	X		X	
Turbinidae	✓					
<i>Haliotis</i>		✓			X	
Caenogastropoda						
Calyptraeidae		✓	?	X (one radiation)		? (microhabitat)
Cypraeidae	✓	✓ (peripheral isolates)		X (upwelling coasts)		
<i>Conus</i>	✓	✓ (Cape Verde Is.)		x		
<i>Echinolittorina</i>	✓	4 pairs in E. Pacific				
<i>Nucella</i>		✓	X			
<i>Littorina</i>		✓	X (Pacific)	X		X (Atlantic)
Heterobranchia						
Nudibranchia		✓	X	X (Antarctic <i>Doris</i>)		X (<i>Phestilla</i>)
Sacoglossa		✓				X (host shifts)

proteins and egg receptors in marine animals with internal fertilization remains an open question for future research.

In most of the groups reviewed here, there are many examples of almost entirely sympatric sister taxa or local radiations that are harder to explain by transient allopatry, including the Patellogastropoda, *Littorina*, *Calyptraea*, nudibranchs, and sacoglossans. The frequent occurrence of sympatric sister species in these groups argues that an ecological basis for speciation needs to be carefully considered for marine animals, before assuming that allopatric divergence explains the bulk of speciation in the sea. In several of these taxa, host or microhabitat associations suggest ecological mechanisms by which disruptive selection may act to sunder a population into specialized ecotypes (Table 1). Reproductive isolation can arise through the diverse mechanisms discussed earlier, allowing close relatives to overlap in range.

Life-history transitions to non-planktonic development may also promote speciation “in proximity,” meaning divergence that allows species to form near each other and fast enough to achieve present-day sympatry. Non-planktonic development is associated with local radiations in temperate zones for littorinid and calyptraeid lineages. Loss of a dispersing planktonic phase is also linked to bursts of diversification in tropical groups, including Cape Verde *Conus* and cypraeids that are peripheral to centers of Indo-Pacific diversity; these groups otherwise show patterns consistent with allopatric speciation across archipelagos. Direct development reduces the spatial scale at which selection acts, increasing local adaptation and likely promoting divergence among ecotypes or populations. The synergistic effects of niche diversification and non-planktonic development should receive attention through comparative studies that control for phylogenetic effects, to test whether this one-two punch indeed promotes speciation.

Although inferring the geography of speciation will remain difficult, phylogenies of marine gastropods illustrate that sister species are broadly sympatric in many groups. This pattern contrasts strongly with theoretical simulations of allopatric divergence and range shifts, and with empirical results for terrestrial and freshwater taxa. Ecological speciation by disruptive selection, potentially facilitated by loss of a planktonic stage, deserves careful attention in efforts to understand the genesis of marine biodiversity. Whether acting during secondary contact or in sympatry, the role of selection must be better studied to explain why close relatives so often co-occur in the shallow waters of our oceans.

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